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Role contribution of biological nitrogen fixation to future terrestrial net land carbon accumulation under warming condition at centennial scale

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ABSTRACT

Future changes in net land carbon (C) accumulation in the terrestrial ecosystem remain highly uncertain. This uncertainty is mainly due to nitrogen (N) availability not being included in model simulations. N availability is ultimately determined by the balance of N inputs and outputs for the terrestrial ecosystem. Here, as the largest N input pathway, the influence of biological N fixation (BNF) combined with increasing atmospheric carbon dioxide (CO_2) concentration, climate change, and atmospheric N deposition on future terrestrial C sequestration is investigated to the year 2100 using the Community Atmosphere–Biosphere–Land Exchange (CABLE) global land surface model. Projections show a net land C accumulation increase of ~20% by 2100 for the terrestrial ecosystem, relative to the pre-industrial (1901–1910) level. BNF will increase terrestrial C sequestration by ~104 Pg C by the end of this century, accounting for ~28% of the total increase in net land C accumulation due to increasing CO_2, climate change, BNF, and atmospheric N deposition. Therefore, the findings highlight the fundamental importance of BNF in determining the size of future net terrestrial C accumulation, although there are still unresolved questions regarding BNF and its role in forecasting climate change. Furthermore, a climate warming-induced increase in soil N mineralization of ~431 Tg N per °C is estimated, resulting in increased N uptake (~17 Tg N yr^{-1}) from soil to vegetation by the end of this century, relative to the pre-industrial period, which could offset soil carbon loss due to warming. This highlights the effect of warming-induced N mineralization on land net C accumulation. Thus, BNF variations and warming-stimulated soil mineralization should be included in model simulations of land C carbon sequestration to prevent the effect of N limitation on land C loss being overestimated.

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1. Introduction

There is still large uncertainty in projections of the size of net land carbon (C) accumulation by the end of the 21st century (Friedlingstein et al., 2014; Wieder et al., 2015a). Such long-term changes in land C storage are expected to be mainly influenced by and vary with atmospheric carbon dioxide (CO_2) concentration (Peng et al., 2014; Wennersten et al., 2015) combined with climate change (Thornton et al., 2007; Dan et al., 2015). The 11 Phase 5 of the Coupled Model Intercomparison Project (CMIP5) Earth system models (ESMs) show a large range for cumulative land C uptake by the end of 21st century, from −165 to 758 Pg C (Friedlingstein et al., 2014). The large uncertainty in land C uptake is partly due to 9 out of the 11 models neglecting nitrogen (N) dynamics. Observations and simulations have shown that N limitation constrains the overestimation of CO_2 fertilization effects (Zaehle et al., 2014; Peng and Dan, 2015). For example, a recent modeling analysis indicated that N limitation is the main driver of the terrestrial biosphere becoming a net C source by 2100, losing 100 ± 200 Pg C to the atmosphere by 2100 (Wieder et al., 2015a). This issue is important as

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the possible influence of variations in land C storage could affect climate change and the atmospheric CO_2 concentration (Al-Mohannadi and Linke, 2016; Zhang et al., 2018).

It is well known that land C storage is affected by N limitation. A model analysis showed that the influence of nutrient limitation on net primary production (NPP) could cause a reduction in land cumulative C uptake (Wieder et al., 2015a). However, another study found that this reduction in C storage is not sufficient to compensate for the strength of CO_2 fertilization. The study projected an increase in net land C accumulation of about 200 Pg C between 1860 and 2100 when N dynamics were included in the O-CN land-surface model (Zaehle et al., 2010). Nevertheless, the results of Wieder et al. (2015a) should be viewed with caution because a static method and stoichiometry were used to estimate the effect of N limitation on the C cycle based on the assumption of an increased N deficit due to increased NPP, without considering the response to climate changes and increased atmospheric CO_2 levels. For example, the mineralization of nutrients is influenced by warming of soil organic matter. In addition, N dynamics should be considered based on changes in the interrelated links with increasing CO_2 and changes in the C:N ratios among various plant organs (Wang et al., 2007; Wang and Houlton, 2009).

In addition, the previous study by Wieder et al. (2015a) used a fixed value for biological N fixation (BNF) and did not consider the effect of variations in BNF. BNF is the dominant natural path through which N enters ecosystems (Vitousek and Field, 2001). It is an enzymatically mediated process that converts N_2 into ecologically available N forms. As the largest natural input of N to land ecosystems globally, BNF already affects the terrestrial C cycle and will continue to do so throughout the rest of this century (Wieder et al., 2015a). However, globally comprehensive analyses of the impacts of increasing CO_2 concentration and climate change on BNF for the end of this century are scarce, especially the effects of BNF change on the global C cycle on the centennial scale (Cleveland et al., 2013; Vitousek et al., 2013; Smith, 2016).

Even though BNF is the largest N input pathway in terrestrial ecosystems, few studies have investigated the impacts of hundred-year BNF, due to lack of an evolving understanding of BNF and the paucity of reliable measurements of this process in the field (Houlton et al., 2008). Here, how changes in BNF combined with increasing atmospheric CO_2 and climate change have modified the regional and global C storage patterns are investigated. Atmospheric N deposition due to anthropogenic emissions is another important pathway for N input to the terrestrial ecosystem. Combining these two pathways, the natural and anthropogenic N contributions to the C cycle in the terrestrial ecosystem are estimated. A terrestrial biophysical and biogeochemical process-based global land surface model (Community Atmosphere–Biosphere–Land Exchange, CABLE) is used to quantify the contribution of the different driving factors (increasing CO_2, climate changes, BNF, and atmospheric N deposition) from 1901 to 2100. There are three principal questions in this study. (1) How does the estimated net land C accumulation change under future climate conditions relative to the pre-industrial level? (2) How does the estimated BNF rate affect land C sequestration globally and among different plant functional types in future? (3) Considering the combined effects of BNF variations, climate changes, atmospheric CO_2, and N deposition, what is the difference in the estimated land C sequestration between the 2100s and the 1900s?

2. Method and simulation

2.1. Estimating BNF

In this study, a resource optimization theory was used to calculate BNF, which was developed by Rastetter et al. (2001), Wang et al. (2007) and Houlton et al. (2008) (see Table 1). It estimates BNF as:

$$BNF_o = \nu_{fix} f_{fix} C_{fix,r} \tau_{root} \quad (1)$$

where ν_{fix} is the rate of N fixation per unit C (g N $(gC)^{-1}$), f_{fix} is the fraction of N_2-fixing plants, $C_{fix,r}$ is the N_2-fixing plant root biomass in g C m^{-2}, and BNF_o is in g N m^{-2} d^{-1}. Under this formulation, the rate of BNF is taken as the product of N fixation per unit C investment (ν_{fix}) and the amount of C invested into BNF.

There are two other commonly used approaches to estimate BNF. For example, using the Community Land Model version 4.5 (CLM4.5bgc) (Thornton et al., 2007), Wieder et al. (2015b) estimated BNF based on a standard NPP–BNF relationship from Cleveland et al. (1999):

$$BNF_{NPP} = 1.8(1 - \exp(-0.003NPP)) \quad (2)$$

where the units are g C m^{-2} yr^{-1} for annual NPP and N m^{-2} yr^{-1} for the annual BNF rate (BNF_{NPP}).

Another approach is based on the evapotranspiration (ET)–BNF relationship, as proposed by Cleveland et al. (1999) (see Table 1), which estimates yearly BNF, BNF_{ET}, using the following equation:

$$BNF_{ET} = 0.00102ET + 0.0524 \quad (3)$$

where annual ET is in mm yr^{-1} and BNF_{ET} is in g N m^{-2} yr^{-1}.

Both the Wieder and Cleveland approaches to modelling BNF rely on empirical correlations and are therefore more phenomenological than mechanistic, and unable to directly address known controls on the process. In contrast, resource optimization approaches are consistent with ecological paradigms of plant C allocation strategies. Hence, in this study, the resource optimization approach is used to estimate BNF at the global and regional scales.

2.2. CABLE version 2 model and forcing data sets

The Community Atmosphere–Biosphere–Land Exchange (CABLE) global land surface model was used to study future changes in net land C accumulation. It has been used to evaluate the effects of nutrient availability on the terrestrial carbon cycle under different representative concentration pathways (RCPs) (Zhang et al., 2014). Assessment of the model performance found that CABLE combined with the CASA-CNP model can well reproduce the annual gross primary production (GPP) estimated by Beer et al. (2010) and global evapotranspiration and annual runoff (Zhou et al., 2012), as well as major global biogeochemical fluxes and the size of the carbon, nitrogen, and phosphorus pools (Wang et al., 2010).

CABLE was applied here at a spatial resolution of 1.9° (latitude) × 2.5° (longitude). For each simulation, the model was spun up by recycling the meteorological forcing from 1901 to 1910 until all carbon and nitrogen pools reached equilibrium (the difference in any pool size between two successive cycles is <0.01%). The equilibrium values of all state variables were used as the initial condition for the 1901–2100 simulation. First, the model was spun up until the carbon pools reached equilibrium, based on the transient climate during 1901–1910, using a constant pre-industrial atmospheric CO_2 concentration of 295.8 ppm. This state was used as the initial condition for the 1901–2100 simulation. Second, historical simulations were run from 1901 to 2004 using climate variables for the period 1901–2004 and CO_2 concentration data for 1901–2004. The model was then run from 1901 to 2004 using transient climate forcing and historical atmospheric CO_2 concentration data. Next, for the period 2005–2100, representative concentration pathway

(RCP) 8.5 forcing was used in the model to assess future changes. We also used N deposition reported by Lamarque et al. (2013).

From 1901 to 2100, the meteorological inputs included temperature, specific humidity, atmospheric pressure, downward solar radiation, downward long-wave radiation, rainfall, snowfall, and wind speed. Meteorological variables from 1901 to 2005 were obtained by re-meshing the 6-h meteorological variables of the GCP-TRENDY data at a spatial resolution of $0.5^\circ \times 0.5^\circ$–$1.875^\circ \times 2.5^\circ$ according to Qian et al. (2006). However, the re-gridded GCP-TRENDY meteorological forcing was interpolated from six-hourly to hourly using the Community Earth System Model (CESM) version 1.0 (Hurrell et al., 2013). From 2005 to 2100, hourly meteorological variables were generated based on the daily means of the corresponding meteorological variables, and the same spatial resolution was generated compared to CESM 1.0 for RCP8.5 (Riahi et al., 2011).

2.3. Experiment design

To estimate the relative contribution of increasing atmospheric CO_2 concentration, climate changes, BNF variations, and atmospheric N deposition, five simulations (S1, S2, S3, S4 and S5) were generated using different input variables for the study period of 1901–2100 (Table 2 and Fig. 1). In the first simulation (S1), atmospheric CO_2, climate variables (e.g., temperature, precipitation, wind), BNF, and atmospheric N deposition were all varied. In the second simulation (S2), atmospheric CO_2 was held constant at the pre-industrial level (295.38 ppm) and the other factors were varied. In the third simulation (S3), climate variables were held constant at the 1901 level and the other factors were varied. In the fourth simulation (S4), the BNF rate was fixed at the 1901 level and the other factors were varied. In the fifth simulation (S5), atmospheric N deposition was held constant at the 1900 level and the other factors were varied.

The difference in land C uptake between simulations S1 and S4 represents the effect of time-varying BNF (S1 – S4, BNF); the effects of atmospheric CO_2 (S1 – S2, CO_2), climate changes (S1 – S3, Cli), and increasing N deposition (S1 – S5, Nd) on land C uptake are estimated as the differences between simulations 1 and 2, simulations 1 and 3, simulations 1 and 5, respectively.

3. Result

The historical period 1959–2004 was selected to compare our model results with data from the Global Carbon Project (GCP) and TRENDY ensemble data, which cover the same period. The estimates of the GCP are the residual land sinks associated with varying fossil fuel, land use, and fire net emissions, the atmospheric CO_2 concentration growth rate, and the oceanic CO_2 sink (Le Quéré et al., 2013). The TRENDY dataset in this study is made up of an ensemble of seven process-based terrestrial ecosystem model simulations (TRENDY experiment S2 without land-use change and fires including CLM4C, CLM4CN, LPJwsl, LPJGUESS, OCN, SDGVM, and TRIFFID here) (Piao et al., 2013). The estimated annual net ecosystem production (NEP) (land carbon uptake) (on average 2.03 ± 1.95 Pg C yr^{-1}) simulated by CABLE (simulation S1) using BNF variations was larger than that estimated by the GCP (1.94 ± 1.02 Pg C yr^{-1}) and TRENDY model ensemble (average 1.57 ± 1.02 Pg C yr^{-1}). Our modeling study only focused on the natural response of the terrestrial ecosystem and did not include land-use change and fires. Hence, not surprisingly, it simulates a larger-than-average land carbon sink than the GCP (Fig. 2). Most NEP of CABLE S1 (1959–2004) falls in the range between 0.57 and 2.60 Pg C yr^{-1} of the TRENDY ensemble data.

Global terrestrial C sequestration during the period 1901–1910, defined as the pre-industrial period in this study, is about 1897 Pg C when considering the combined effects of atmospheric CO_2, climate changes, and N input via BNF and atmospheric N deposition in simulation S1 (Fig. 3a). This value falls into the total global terrestrial C sequestration range of 999–2999 Pg C during the initial period of 1860–1869 from CMIP5 and is comparable to the pre-industrial mean value of ~1859 Pg C from the IPCC AR5 (AR5, 2013). During the historical period of 1995–2004, CABLE-derived total terrestrial C storage is ~2054 Pg C. This value agrees with the simulated range of 956–3334 Pg C (AR5, 2013). On the decadal scale, the average historical terrestrial C sequestration was 15 Pg C during 1980–1989, with a range of 4–26 Pg C, and ~26 Pg C during 1990–1999, with a range of 4–28 Pg C (AR5, 2013), which covers our simulation S1 with an average of 24 Pg C during 1980–1989 and 28 Pg C during 1990–1999 (Fig. 3b and Table 3), respectively. For the longer period of 1901–2005, the cumulative terrestrial C uptake is about 180 Pg C, which falls into the range of 49–229 Pg C

Table 2
CABLE simulations driven by different factors (atmospheric CO_2 concentration, climate changes, biological nitrogen fixation (BNF), and atmospheric N deposition) for estimating land C storage.

Simulation	CO_2	climate	BNF	N deposition
S1	Time-varying	Time-varying	Time-varying	Time-varying
S2	Fixed at 1901	Time-varying	Time-varying	Time-varying
S3	Time-varying	Fixed at 1901	Time-varying	Time-varying
S4	Time-varying	Time-varying	Fixed at 1901	Time-varying
S5	Time-varying	Time-varying	Time-varying	Fixed at 1901

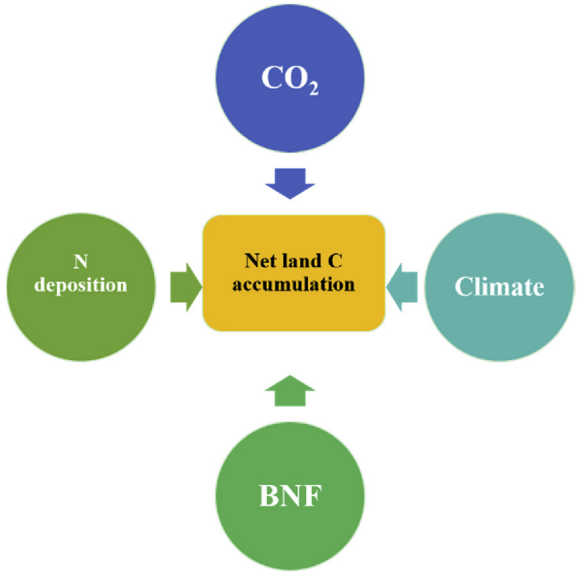

Fig. 1. Simulation scheme using different driving factors in CABLE.

Table 1
Summary of the calculation of BNF and relevant references justifying the chosen parameterization.

BNF approach	f(NPP)	f(ET)	f(N fixation per unit C investment, C root, temperature et al.)
Reference	Wieder et al. (2015b)	Cleveland et al., 1999	Wang et al., 2007, Houlton et al., 2008

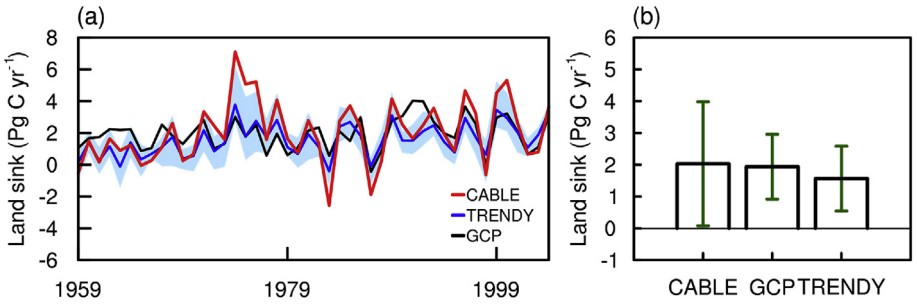

Fig. 2. (a), Interannual variations in land C sink simulated by CABLE (red line), GCP (black line), and TRENDY (blue line) during 1959–2005. (b), Averages of CABLE, GCP, and TRENDY for 1959–2005. Data are mean ± SE calculated from simulated values over the entire period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

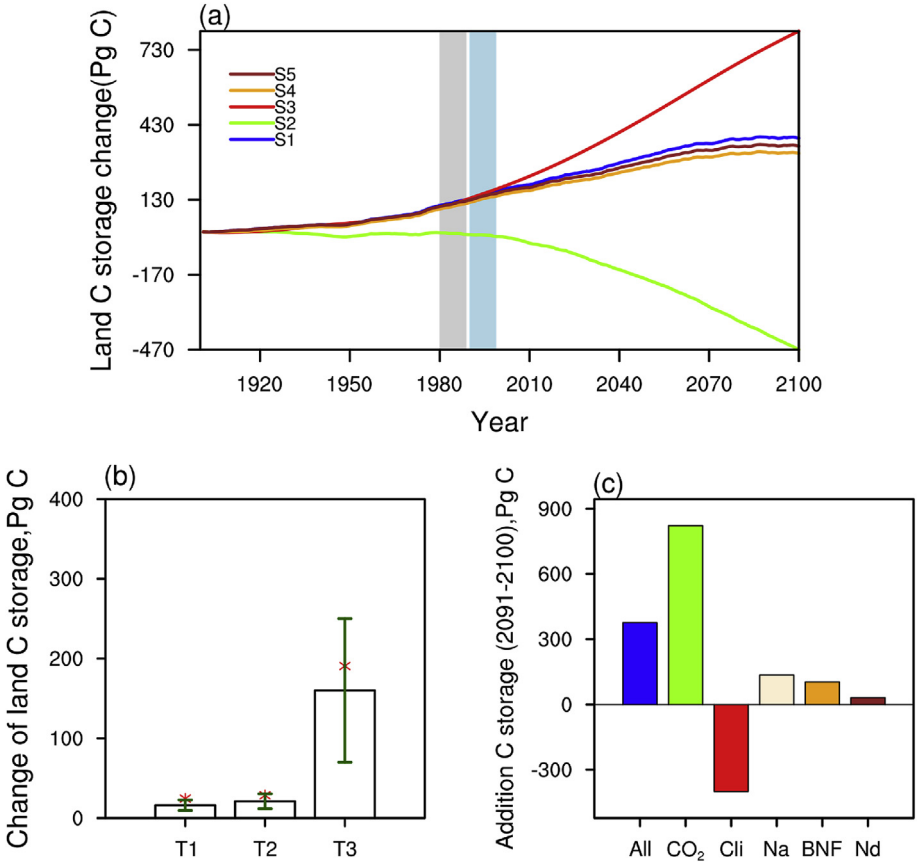

Fig. 3. (a) Changes in net land C accumulation for simulations S1, S2, S3, S4, and S5 during 1901–2100. The gray bar covers the historical period of 1980–1989 and the light blue bar covers the period of 1990–1999. (b) For three stages T1 (1980–1989), T2 (1990–1999) and T3 (pre-industrial stage to 2005), comparisons of changes in net land C accumulation between CABLE S1 (red star) and CMIP5 (black bar). The vertical dark green lines denote mean ± SE calculated suggested by IPCC AR5 (2013). (c) Changes in net land C accumulation due to different driving factors during 2091–2100 relative to the pre-industrial period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

estimated for the land-use change carbon flux by 11 Earth system models (ESM) during 1850–2005 (Friedlingstein et al., 2014) and the range of 70–250 Pg C during 1750–2011 from IPCC AR5 (2013).

The change in terrestrial C sequestration during 2091–2100 relative to 1901–1910 is estimated to be 376 Pg C (S1) when considering the combined effects of increasing atmospheric CO_2, climate changes, atmospheric N deposition, and BNF variations. To investigate the contribution of each of these factors, five simulations were conducted. As the most important pathway of N input into the terrestrial ecosystem, changes in BNF increased terrestrial C storage by 104 Pg C during 2091–2100, relative to the initial level during 1901–1910 (S1–S4) (Fig. 3c). This contribution is smaller compared with modeled changes in terrestrial C storage due to climate change (a reduction of C sequestration of approximately −400 Pg C), and the enhancement of plant productivity due to the CO_2 fertilization effect (an increase of ~822 Pg C). As another pathway of N input into the terrestrial ecosystem, atmospheric N deposition plays a relatively minor role. However, it still contributes an increase in C sequestration of 32 Pg C by the end of this century, which is close to the results of Zaehle et al. (2010). BNF and atmospheric N deposition interact with the C cycle via one main pathway: the terrestrial N cycle receives inputs, which

Table 3
Historical net land C accumulation simulated by CMIP5 compared with the CABLE simulation.

Model names	Time periods	Net land C accumulation (PgC)		
		Min	Max	Average
CMIP5	T1 (1980–1989)	4	26	15
	T2 (1990–1999)	4	28	26
	T3 (pre-industrial stage to 2005)	49	229	124
CABLE	T1 (1980–1989)			24
	T2 (1990–1999)			28
	T3 (pre-industrial stage to 2005)			180

directly influence the terrestrial N availability and N balance. The N input (sum of BNF and atmospheric N deposition) leads to a total increase in terrestrial C storage of ~136 Pg C by the end of this century relative to 1901–1910, which accounts for ~36% of the global land increase in C sequestration caused by all the factors combined by the end of this century, relative to the pre-industrial level.

Across the global land surface and even within biomes, the spatial distribution of net land C accumulation by the end of this century (2091–2100) (Fig. 4a) and its changes during the same period relative to the pre-industrial level (1901–1910) (Fig. 4b) varies considerably due to different factors. For instance, C sequestration has an average increase in the tropical forest ecosystem, but variability within this biome is high, ranging from a decrease of −9 kg C m^{-2} to an increase of 12 kg C m^{-2}. This likely reflects that productivity is more limited by heat stress than enhanced by the CO_2 fertilization effect in this biome compared with other biomes (Fig. 4c). In addition, using the CABLE model, a strong latitudinal variance in C sequestration is detected, mainly via strong regulatory effects on net land C accumulation due to changing climatic factors (Fig. 4d). For example, north of 40°N, surface warming has a positive effect on C sequestration, whereas in the tropical forest ecosystem, which is mainly covered by evergreen broadleaf forest (EBF), local C sequestration is driven by heat-stress-related C losses via an increase in soil respiration of ~25 Pg C yr^{-1}. As a result, C loss in soil offsets ~16% of the increase in net land C accumulation.

BNF variations contribute a moderate increase in terrestrial C storage (S1–S4) (Fig. 4e). Based on previous estimations, Cleveland et al. (1999) reported that total terrestrial BNF is about ~195 Tg N yr^{-1} globally. This agrees with our current estimation of 124 Tg N yr^{-1} during the period 1985–1994. The modeled increase in BNF rates mainly results from increasing atmospheric CO_2 (16 Tg N yr^{-1} per 100 ppm), which agrees with a previous estimation (ranging from −2 to 28 Tg N yr^{-1} per 100 ppm) (Meyerholt et al., 2016). According to our simulations, BNF-induced changes in terrestrial C sequestration account for 28% of the global increase caused by all factors combined. To date, estimations of both the trend and variability of the future BNF contribution to C storage are rare under warming conditions and increasing atmospheric CO_2 concentration. In accordance with our simulation results, our model can simulate a range of BNF regulation strategies among different biomes. A significantly greater increase in net land C accumulation is found in most boreal forest regions, such as in northern America and northern Europe, which are the key regions affected by N limitation. In contrast, regions with a smaller N deficit, such as most of the Amazonian region, southeastern Asia and northern Africa, show a negligible change in C sequestration. Although C sequestration in tropical forests (EBF), such as the Amazonian region and southeastern Asia, does not significantly change by 2100 relative to the 1900s due to local BNF, regional C storage increases from 14 to 22 Pg C, coincident with enhanced BNF in deciduous broadleaf

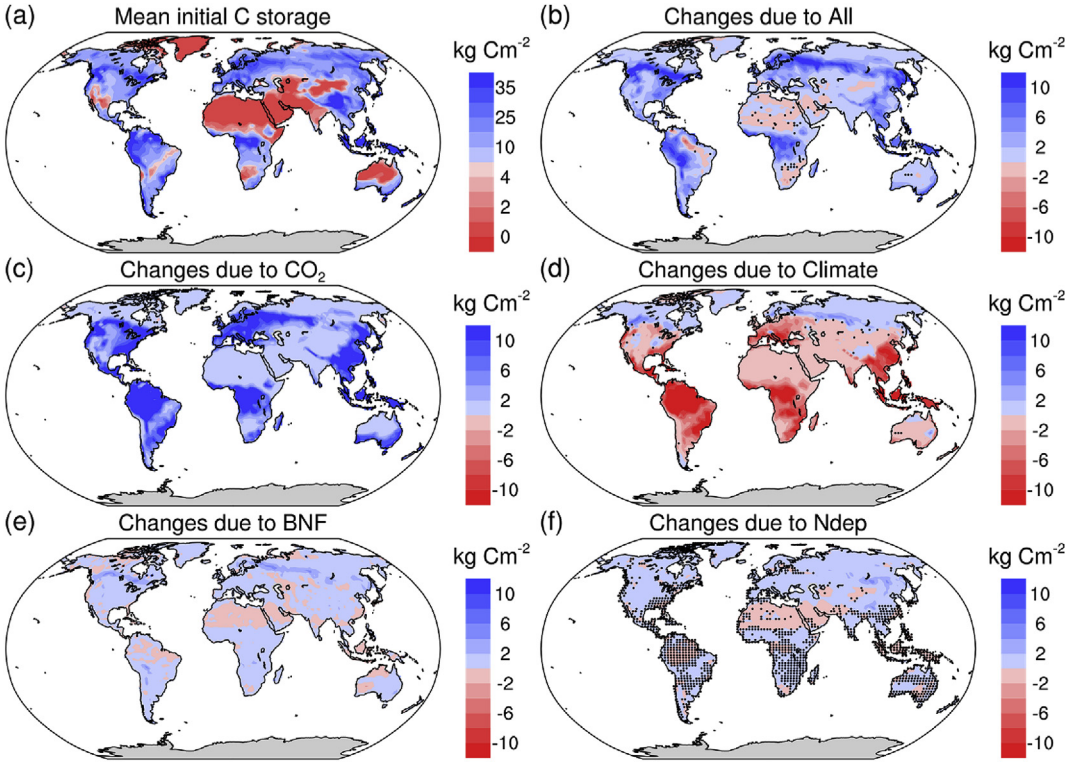

Fig. 4. (a) Spatial distribution of mean terrestrial C storage for 1901–1910. (b) Differences in C storage during 2091–2100 relative to 1901–1910 from simulation S1. (c) Changes due to increasing CO_2 concentration. (d) Changes due to climate changes. (e) Changes due to BNF. (f) Changes due to atmospheric N deposition. Black dotted areas are regions where changes are not statistically significant at the 95% confidence level using the Student's *t*-test; other regions passed the 95% confidence level.

forest (DBF), which are typically N-limited regions.

Furthermore, although atmospheric N deposition rates have been increasing in recent decades, and are projected to continue increasing, they account for only a small proportion of annual N nutrition globally, relative to BNF (~45%). The increase in atmospheric N deposition still contributes a slight increase to the terrestrial C sequestration by the end of this century (Fig. 4f). It especially enhances C sequestration between 40°N and 60°N, where the strongest anthropogenic atmospheric N deposition occurs. The atmospheric N deposition effect on terrestrial C sequestration by the end of this century is significantly greater in central Europe and northern Asia, in which evergreen needleleaf forest (ENF) and deciduous broadleaf forest (DBF) are expected to dominate the sequestration process. In these regions, the contribution of increased atmospheric N deposition accounts for up to 10–23% of the C storage. A previous study also supports the result that, historically, increased atmospheric N deposition in these northern temperate regions could have stimulated the accumulation of forest biomass (Nadelhoffer et al., 1999). Conversely, the N deposition-driven C sequestration is not significant in most tropical forest ecosystems where N is plentiful. It is expected that N limitation will make a slight contribution to C sequestration in these regions: N input in tropical ecosystems via BNF and atmospheric N deposition plays a rather small role, whereas it plays a vital role in boreal ecosystems, and a robust role in temperate ecosystems.

Expressed as the sum of plant, litter, and soil C storage, the C sequestration change determined using different forcing factors for three different biomes and the global terrestrial ecosystem is presented in Fig. 5(a)–(p). All biomes display a significant increase in C sequestration in S1, but the relative contributions of the different factors are not constant. For example, the CO_2 fertilization effects (S1 minus S2) are the key cause of the increase in net land C accumulation in the temperate forest ecosystem (162 Pg C). In this region, a decrease in C sequestration (−128 Pg C) occurs when only the effects of climate change are considered (S1–S3) by the end of this century. This indicates that surface warming alone does not benefit plant growth and induces a reduction in the plant C pool of ~59 Pg C and a decrease in the soil C pool of ~48 Pg C in this region by the end of this century. In addition, N inputs via BNF and atmospheric N deposition play a key role, representing ~31% of the total increase in C sequestration (~26 Pg C) in the same period, although its magnitude is smaller than that influenced by atmospheric CO_2 concentration and climate change, respectively.

For evergreen needleleaf forest, an increase in C sequestration (accounting for ~30% of total land C sequestration) in S1 is predicted. In this biome, in response to climate change only, plant C storage increases by ~9 Pg C, which offsets part of the decrease in C loss in soil caused by increasing temperature (~16 Pg C). N inputs via BNF and atmospheric N deposition make a significant contribution to this total enhancement (~22% or 25 Pg C). In addition, for the tropical biome, an increase in C sequestration accounts for 34.4% of the total global C sequestration increase, and the CO_2 fertilization effect is the main contributor to the increase in C sequestration (~378 Pg C), whereas a decrease is seen when considering climate changes only (~−180 PgC). Such a reduction is not sufficient to compensate for the CO_2-fertilization-induced increase in plant, soil, and litter C storage. As a result, the combined opposing effects of increasing atmospheric CO_2 and heat stress in these regions, such as in southeastern Asia, still induce an increase in C sequestration during 2091–2100 (16 Pg C).

4. Discussion

Taking into account N effects, CABLE still simulates a large increase in net land C accumulation projection of more than ~350 PgC by the 2100s under the RCP8.5 scenario. It agrees with the sign of changes in net land C accumulation by the end of this century reported by Zaehle et al. (2010) (Fig. 6a). In addition, the combined effect of all factors on modeled net land C accumulation is positive and in overall agreement with independent results from modeling studies of climate–CO_2 interactions (Thornton et al., 2007; Friedlingstein et al., 2014). However, the results differ from Wieder et al. (2015b), who reported that N limitation will result in a C storage decrease and that the terrestrial ecosystem will become a large C source, losing 140 ± 240 PgC to atmosphere by the end of this century, relative to the pre-industrial level. The difference can be attributed to the large spread of differences in model processes, and the importance of these processes to land C storage have been validated by models and observations (Melillo et al., 2011; Cleveland et al., 2013; Meyerholt et al., 2016).

First, N inputs via BNF and atmospheric N deposition play a substantial role in C sequestration, especially in N-insufficient regions, which has been indicated by previous analyses (Cleveland et al., 1999; Houlton et al., 2008). BNF is the dominant natural path through which N enters ecosystem (Vitousek and Field, 2001), an enzymatically mediated process that converts N_2 into ecologically available N forms. Consistent with previous studies (Wang and Houlton, 2009; Cleveland et al., 2013; Meyerholt et al., 2016), simulation S1 showed a positive effect of changes in N input via N fixation and N deposition on net land C accumulation. Only considering the effect of BNF (S1–S4), strong increased BNF (Fig. 6b) induced a parallel growth of the net land C accumulation. This supports the conclusion that enhanced BNF regulates the net land C accumulation through enhanced N input into the terrestrial ecosystem as mentioned above, representing about 28% of the total global increase in land C storage by the end of this century relative to the 1901 level. This effect of N input mainly via N fixation counteracts the effect of N limitation on CO_2 fertilization and C storage for the terrestrial ecosystem by the end of this century. This process of BNF variation is not reflected in the models used by Wieder et al. (2015a), which only include fixed BNF. Therefore, without variation of BNF the effect of N limitation on future net land C accumulation is likely overestimated.

Second, warming is a key factor controlling soil mineralization from soil organic matter. Enhanced soil mineralization in response to warming (simulations S1–S3) has been illustrated. Considering the warming effect, soil N mineralization change can be expressed as a function of temperature change relative to pre-industrial levels: $Nsmin_i - Nsmin_{i0} = a(T_i - T_{i0}) + b + \varepsilon$, where $Nsmin_i$ is the value of soil mineralization by 2100, $Nsmin_{i0}$ is the pre-industrial value of the soil mineralization, T_i is the surface temperature by 2100, T_{i0} is the preindustrial value of surface temperature, a is the annual linear trend, b is the intercept, and ε is the residual error. This simplified equation assumes a linear relationship between soil mineralization and surface temperature. If a is >0 and the Pearson correlation coefficient (P) is <0.05, a significantly increased soil mineralization linear trend in response to increasing temperature of ~431 Tg N per °C is predicted (Fig. 6c). Such a relationship between soil N mineralization and increasing temperature has also been observed in warming experiments in a range of ecosystems (Melillo et al., 2011). As a consequence, although soil warming causes loss of carbon from the soil, it leads to increased nutrient availability due to enhanced soil N mineralization and could compensate the carbon loss caused by warming. If an increase in soil mineralization in response to increasing temperature is reflected, then an accompanying increase in plant N uptake (17 Tg N yr^{-1}) from soil to vegetation is suggested by CABLE S1 by the end of this century, relative to the pre-industrial level. These results have important implications for the stimulation of land

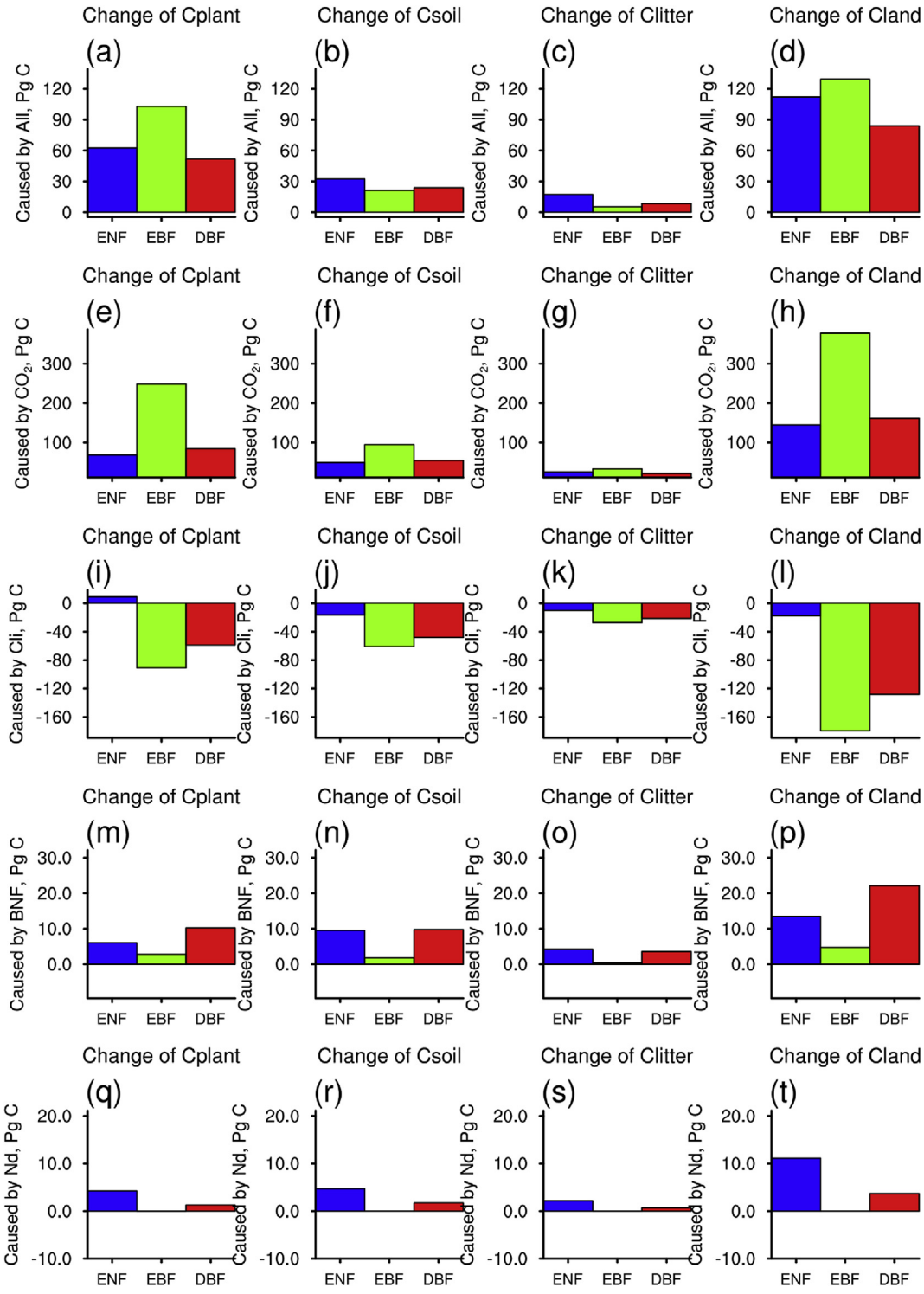

Fig. 5. Changes in the net plant C, soil C, litter C, and land C accumulation for typical plant functional types, evergreen needleleaf forest (ENF), evergreen broadleaf forest (EBF) and deciduous broadleaf forest (DBF), caused by the combined effect of all factors (All) ((a)–(d)), increasing CO_2 concentration (CO_2) ((e)–h)), climate changes (Cli) ((i)–(l)), changes in biological N fixation (BNF) ((m)–(p)), and atmospheric N deposition (Nd) ((q)–(t)) during 2091–2100 relative to 1901–1910.

carbon storage via increased nutrient availability. Therefore, without the warming-induced effect on soil N mineralization, the impact of N limitation on C loss under warming conditions would be overestimated (Wieder et al., 2015a, 2015c).

Third, there are some other important problems, such the allocation of C among leaf, woody tissue, and roots in response to nutrient change, that are not included in the previous study (Wieder et al., 2015a). If there is an increase in roots in response to nutrient limitation, this could increase root uptake of mineral nutrients. As shown in simulation S1, the C fraction of roots increases by 3% by the end of this century relative to the pre-industrial level (Fig. 6d). Such changes in plant C allocation can exert a positive effect on N access. Iversen et al. (2008) found that increased CO_2 only led to an increase in root C and N in free-air CO_2 enrichment

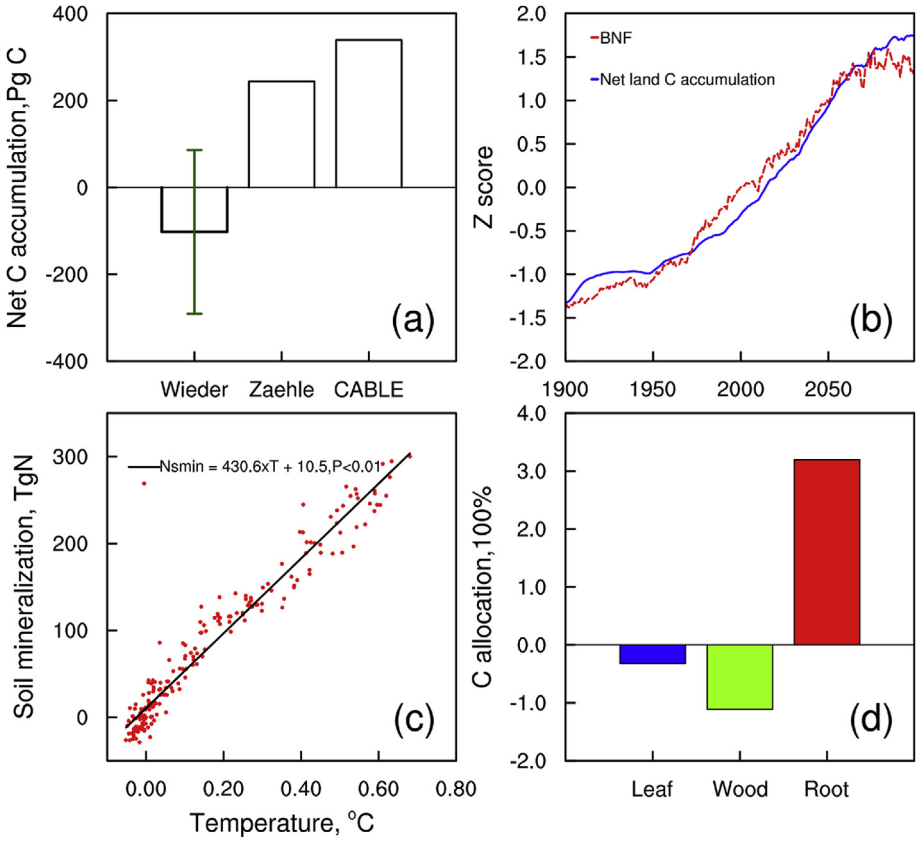

Fig. 6. (a) Changes in net land C accumulation by the end of this century relative to the pre-industrial level. Vertical dark green lines denote mean ± SE calculated suggested by Wieder et al. (2015a). (b) Annual net land C accumulation and BNF anomaly, as *Z* score simulated by CABLE for 1901–21005. (c) Relationship between changes in soil N mineralization and surface temperature during 1901–2100. (d) Percent changes relative to pre-industrial level in modeled C allocation of leaf, wood, and root. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(FACE) experiments. This C allocation strategy under nutrient limitation could help to stimulate soil N availability in response to the increased CO_2 observed in FACE experiments; however, there are many uncertainties in the C allocation processes in plants on the large scale, including the magnitude of belowground biomass (Zaehle et al., 2014).

In addition, it should be noted that uncertainties still exist in the size of the net land C accumulation by the end of this century relative to the pre-industrial level. For example, phosphorus (P) also plays an important role in the global C–N cycle, particularly in the tropical forests of the Amazon, Congo, and southeastern Asia, but knowledge at present about its potential contribution to C sequestration on a global scale is still limited. A previous study suggested that P limitation will continue to constrain C storage in the terrestrial biosphere in the future (Wieder et al., 2015a). Therefore, global change of net land C accumulation may be suppressed when P dynamics are included, especially in tropical forest. Further work based on spatial and temporal P dynamics are needed to quantify its role in net land C accumulation in global C–N–P cycles.

5. Conclusion

This study used a recently developed ecosystem model to predict future changes in terrestrial C sequestration, and showed that composite responses of net C accumulation in future vary with increasing atmospheric CO_2 concentration, climate changes, and N input changes via BNF and atmospheric N deposition. The key results are summarized as follows.

Global C sequestration via C–N interactions has increased under increasing atmospheric CO_2 concentration and climate change. An increase in C sequestration of ~20% globally is expected by the end of this century relative to pre-industrial level.

N inputs, mainly via BNF, strongly influence future global net land C accumulation, especially in the most N-limited regions, with a C sequestration increase that accounts for 36% of the net land C sequestration increase globally. In particular, increases in BNF by 2100 relative to 1901 could account for about 28% of the increase in land C accumulation due to combined effects of increasing CO_2, climate changes, BNF, and N deposition. A previous study only used fixed BNF and did not consider the effect of BNF variations on net land C accumulation, therefore potentially overestimating the effect of N limitation on net land C accumulation. Hence, BNF variations should be included in projections of the global land C cycle.

While global terrestrial ecosystems show enhanced C sequestration by the end of this century, results also suggest that current global warming has already begun to accelerate C loss in tropical and temperate biomes, offsetting between ~48% and ~79% of the increase caused by CO_2 fertilization effects. However, under warming conditions, N mineralization likely has a positive response of about ~431 Tg N per °C. Enhanced soil mineralization resulting from soil warming could potentially compensate the soil carbon loss due to the effect of warming.

Author contributions

J.P. and L.D. designed the study and wrote the manuscript. Y.W. modified the manuscript. X.Y., X.T., F.Y. processed and analyzed the

data. J.P., X.L. and B.P. provided the data. All authors reviewed the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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